Small-scale variation of plant traits in a temperate forest understorey in relation to environmental conditions and disturbance

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Abstract: Functional trait-based approaches have been increasingly employed to study both plant responses to and effects on ecosystem processes. Knowledge about the links between associated traits and environmental factors may improve our understanding of the mechanism behind ecosystem functioning and change. Various analyses of biological traits in response to complex environmental gradients as well as large-scale screenings have revealed recurrent patterns of trait associations across different ecosystems. The present study, however, focuses on small-scale variation. In Austria's Northern Limestone Alps, temperate montane forest understorey was analysed on a small scale by combining species abundance and environmental data with a set of twelve soft as well as hard traits measured or collected from literature for the more frequent vascular understorey plants. In a direct trait-based approach the link between plant traits and environmental conditions was explored using a three-table ordination technique, namely RLQ analysis. A clear separation between different functional specifications along the first RLQ axis could be demonstrated as a trade-off between traits associated with resource acquisition and resource conservation, respectively. The significant relationship between species traits and environmental variables was highlighted by a functional shift between two environmentally different subareas. Trait specifications in response to different abiotic conditions and disturbance intensities are discussed in view of small-scale resource acquisition strategies. Moreover, the distribution of C-S-R plant strategies and their associated trait specifications are discussed in relation to disturbance and stress-tolerance.

Zusammenfassung: Wissenschaftliche Untersuchungen, die sowohl die Reaktionen als auch Effekte der Vegetation auf ökosystemare Prozesse analysieren, fokussieren zunehmend auf funktionelle Eigenschaften der Pflanzen. Die vorliegende Studie befasst sich mit der Variabilität funktioneller Eigenschaften im krautigen Unterwuchs eines montanen Karbonat-Buchenmischwaldes der Nördlichen Kalkalpen Österreichs. Auf räumlich feinem Maßstab wurden Vegetationsdaten (Abundanzdaten) und Umweltvariablen erhoben. Zusätzlich wurden für die vorkommenden Pflanzenarten Informationen zu zwölf funktionellen Eigenschaften aus verschiedenen Literaturquellen kompiliert. Der Zusammenhang zwischen den funktionellen Eigenschaften der Pflanzen und den abiotischen Standortsfaktoren wurde dann mittels einer Drei-Tabellen-Ordination (RLQ-Analyse) der kombinierten Datensätze analysiert. Entlang des Umweltgradienten ließ sich eine klare Trennung zwischen unterschiedlichen funktionellen Spezialisierungen feststellen, welche zwei grundlegende Möglichkeiten der Ressourcen-Allokation repräsentieren. Auf der einen Seite stehen Pflanzen, die zum möglichst hohen Ressourcenerwerb in schnelles Wachstum und hohe Photosyntheseraten investieren, und auf der anderen Seite solche, deren funktionelle Eigenschaften zu Ressourcenspeicherung und höherer Widerstandsfähigkeit führen. Der Zusammenhang zwischen den Eigenschaften der Pflanzen und den Standortsfaktoren wird gemeinsam mit der Verteilung von C-S-R Strategietypen im Untersuchungsgebiet diskutiert. Kenntnisse über die Abhängigkeit pflanzlicher Strategietypen von Umwelteigenschaften sind für Vorhersagen über die Vegetationsentwicklung im Angesicht der globalen Veränderungen essentiell. Solche Vorhersagen sind notwendig, um zielgerichtete umweltpolitische Maßnahmen setzen zu können.

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Introduction

Community ecology has increasingly focused on biological traits rather than taxonomy-based approaches, which has particularly become evident in the recent efforts to compile comprehensive plant trait databases, for example LEDA (Kleyer, Bekker et al. 2008), BIOFLOR (Klotz, Kühn et al. 2002), CLOPLA (Klimesova and Klimes 2007), and BIOPOP (Poschlod, Kleyer et al. 2003). The advantage of functional approaches is that results and ecological conclusions may be compared beyond phytogeographical boundaries of species pools (Verheyen, Honnay et al. 2003), thus helping to understand what drives vegetation change and ecosystem processes in different parts of the world (Grime 2001). In this context, so-called "hard traits", mainly physiological plant characteristics like relative growth rate or leaf nitrogen content, have been proven to affect ecosystem functions such as biogeochemical cycling (Díaz, Hodgson et al. 2004 and references therein). Hard traits are laborious to measure compared to "soft traits", which comprise morphological or life-history traits such as growth form or life span (Hodgson, Wilson et al. 1999; Lavorel and Garnier 2002; Díaz, Hodgson et al. 2004). As soft traits are easier to evaluate on a large scale, their usage would be convenient in ecosystem ecology but, so far, no direct effect of soft traits on ecosystem functioning has been shown. Nevertheless, the application of soft traits in the study of plant functional responses as well as their influence on ecosystem processes is useful because soft traits are indicative of hard traits owing to correlations between them (Lavorel and Garnier 2002; Díaz, Hodgson et al. 2004). As plant species possessing the same kind of functional traits will respond similarly to major environmental processes, knowledge about plant trait-environment relations can be used to predict community and ecosystem processes, which will be essential for conservation of different vegetation types but also to preserve ecosystem functions and services in view of global change (Noble and Gitay 1996; Díaz and Cabido 1997; Kahmen and Poschlod 2004).

Extensive research on functional diversity has been conducted in response to various environmental conditions, especially soil nutrient availability, disturbance, shading, climate, and CO_2 (Lavorel and Garnier 2002 and references therein). In the course of these studies, recurrent associations between traits have been demonstrated in various ecosystems indicating a fundamental trade-off between traits relevant to resource acquisition and conservation, respectively (Grime 1977; Chapin 1980; Reich, Walters et al. 1992; Díaz and Cabido 1997; Grime, Thompson et al. 1997; Díaz, Hodgson et al. 2004; Kazakou, Garnier et al. 2007; Navas, Roumet et al. 2009). However, our study evaluates the relevance of such trade-offs for shaping the functional composition of vegetation at a local scale.

A functional approach for studying correlations between vegetation and environment may either be based on directly evaluating the relationships between traits and environmental conditions or involve functional classifications of plants sharing similar traits. Among these functional groupings the most widely used classifications are "emergent groups" (Lavorel, McIntyre et al. 1997), "plant functional types (PFT)" (Noble and Gitay 1996; Lavorel and Garnier 2002), and most notably "plant strategies" (Grime 1977). However, it has been emphasized (Lavorel and Garnier 2002; Aubin, Ouellette et al. 2009) that direct trait-based approaches are more accurate and applicable to explore the links between vegetation and environment. Direct functional analyses link species traits with environmental variables through species abundance data, thus simultaneously incorporating three data matrices (Dray and Legendre 2008; Aubin, Ouellette et al. 2009). By now (Aubin, Ouellette et al. 2009) we know three statistical techniques that are able to do so, namely double CCA (Lavorel, Touzard et al. 1998), fourth-corner analysis (Legendre, Galzin et al. 1997), and RLQ analysis (Dolédec, Chessel et al. 1996). In this study, we apply RLQ analysis to understorey data of a temperate, montane forest in the Northern Limestone Alps (Austria). RLQ analysis has

Table 1: List of analysed species and respective abundance units (functional or morphological units) depending on the species growth forms that were recorded in addition to species cover at each vegetation plot. Abundance units were used to evaluate prevalence of species by calculating the ratio of species cover to the number of abundance units for each vegetation plot, and additionally dividing this ratio by the sum of leaf, needle, and mineral soil cover values (Table 2).

Species	Abundance Unit
Actaea spicata	Individuals
Adenostyles alpina	Ground leaves (of rosette)
Asarum europaeum	Ground leaves (of rosette)
Bellidiastrum michelii	Ground leaves (of rosette)
Brachypodium sylvaticum	Vegetative shoots
Calamagrostis varia	Vegetative shoots
Cardamine trifolia	Ground leaves
Carex alba	Vegetative shoots
Carex digitata	Vegetative shoots
Carex flacca	Vegetative shoots
Carex pendula	Vegetative shoots
Carex sylvatica	Vegetative shoots
Cyclamen purpurascens	Ground leaves (of rosette)
Daphne laureola	Individuals
Daphne mezereum	Individuals
Euphorbia amygdaloides	Vegetative shoots
Fragaria vesca	Ground leaves
Galeobdolon montanum	Vegetative shoots
Galium odoratum	Vegetative shoots
Galium rotundifolium	Vegetative shoots
Helleborus niger	Ground leaves (of rosette)
Hordelymus europaeus	Vegetative shoots
Knautia maxima	Ground leaves (of rosette)
Luzula pilosa	Vegetative shoots
Lysimachia nemorum	Vegetative shoots
Mercurialis perennis	Vegetative shoots
Oxalis acetosella	Ground leaves
Phyteuma spicatum	Ground leaves (of rosette)
Polygonatum verticillatum	Vegetative shoots
Prenanthes purpurea	Vegetative shoots
Primula elatior	Ground leaves (of rosette)
Rubus idaeus	Shoots
Sanicula europaea	Ground leaves (of rosette)
Senecio ovatus	Vegetative shoots
Sesleria albicans	Vegetative shoots
Valeriana tripteris	Ground leaves (of rosette)
Viola reichenbachiana	Ground leaves (of rosette)

Table 2: Categories of soil surface matter: At each vegetation plot percentage of covered soil surface by each category was estimated. On the one hand, these cover values were used to account for variation in humus quality between vegetation plots by calculating the ratio of leaves to needles cover values (ratio L/N) and, on the other hand, to account for rock and aboveground root surfaces in the calculation of species prevalence (Table 1).

Category	Explanation
Leaves	Leaves from deciduous trees (especially *Fagus sylvatica, Acer pseudoplatanus, Fraxinus excelsior*); also green leaves
Needles	Needles from conifers (especially *Picea abies*); also green needles
Mineral soil	Bare soil, i.e. no humus on mineral soil surface
Else	e.g. roots, deadwood, rock, stumps

already been used successfully in other plant ecological studies (Bᴀʀʙᴀʀᴏ, Cᴏʀᴄᴋᴇᴛ et al. 2000; Cʜᴏʟᴇʀ 2005; Tʜᴜɪʟʟᴇʀ, Rɪᴄʜᴀʀᴅsᴏɴ et al. 2006; Bᴇʀɴʜᴀʀᴅᴛ-Rӧᴍᴇʀᴍᴀɴɴ, Rӧᴍᴇʀᴍᴀɴɴ et al. 2008). A set of soft as well as hard traits (Table 3) is analysed in relation to several environmental attributes. In particular, we aim to test if (1) there is a significant relationship between traits of temperate forest herbs and environmental attributes; (2) temperate forest herbs display a functional trade-off between resource acquisition and conservation traits on a small scale; (3) C-S-R plant strategies (Gʀɪᴍᴇ 1977) are in line with this functional shift. In addition, we discuss our results with respect to different anthropogenic disturbance intensities between two subareas of the study site.

Material and Methods

Study area

The ecosystem monitoring site „Zöbelboden" is Austria's Integrated Monitoring (IM) site within the UN-ECE International Cooperative Programmes (ICP) on "Integrated Monitoring of Air Pollution Effects on Ecosystems" and also part of the Long-Term Ecological Research Network (LTER) Austria. The approximately 90 ha large site is situated in the central part of Austria (N 47° 50' 30'', E 14° 26' 30'') at the northernmost edge of the Northern Limestone Alps and is part of the Limestone Alps National Park since 1998 (Figure 1). Long-term averages of temperature and precipitation are + 7.2°C and 1650 mm/year, respectively, allowing a vegetation period of around 190 days/year. The bedrock is formed by Calcitic dolomite, which is overlaid by a wide variety of limestone in some areas. Vegetation and soil data were collected from an almost flat plateau (850-956 m.a.s.l., intensive plot 1, IP1 henceforth), on the one hand, and a steep slope (550-850 m.a.s.l., intensive plot 2, IP2 in the following), on the other hand. Predominating soils consist of those on relict loams (Chromic Cambisols and Hydromorphic Stagnosols) at the plateau and of shallow calcareous soils (Lithic and Rendzic Leptosol) at the slope (FAO/ISRIC/ISSS 2006). At the slope, the mixed montane forest with beech *(Fagus sylvatica* L*.)* as the dominant species (*Adenostylo glabrae-Fagetum* sensu Wɪʟʟɴᴇʀ (2002)) can be regarded as natural vegetation. At the plateau, forests are actually dominated by Norway spruce (*Picea abies* (L.) Kᴀʀsᴛ.) after a clear-cut and subsequent plantation of the species around 1910. Recent bark beetle infestation necessitated single tree harvesting. The potential natural vegetation of the plateau is a mixed montane forest with *Fagus sylvatica,*

Picea abies, and European Silver Fir (*Abies alba* Mɪʟʟ.), (*Cardamino trifoliae-Fagetum* sensu Wɪʟʟɴᴇʀ (2002)).

Collection of species and litter data

Vegetation data were collected in July and August 2007. Both IP 1 at the plateau area and IP 2 at the slope, were divided into a regular 5m grid. Within each of the resulting 25m^2 subareas (31 at IP 1 and 32 at IP 2) two vegetation plots á 0.5 x 0.5 m were randomly selected delivering 107 vegetation samples in total (Figure 2, Figure 3). The remaining plots have not been sampled due to recent windthrow disturbance. Observations were carried out using a wooden frame with an inner dimension of 0.5 x 0.5 m that was placed directly on the forest floor at each plot. To facilitate recording of the vegetation on a small-scale the frame was divided into 25 subplots á 10 x 10 cm via adjustable cords that allowed regular and stable sizes without damaging bigger plant parts (Figure 4). For documentation purposes each vegetation plot was photographed (Casio EXILIM, smc PENTAX ZOOM lens/optical 3x, 5.8 – 17.4 mm).

Species as well as litter data were collected in each subplot. Abundance of each species of higher plants (Spermatophytes) was assessed using two different approaches: Species cover as percentage of ground covered by above ground plant parts, on the one hand, and functional or morphological units (abundance units), on the other hand. As far as the latter is concerned, different units such as vegetative shoots, ground leaves in a basal rosette, or simple individuals were counted depending on each species' growth form (Table 1). Abundance units that covered more than one subplot (e.g. a ground leaf from a rosette of True oxlip, *Primula elatior* (L.) Hɪʟʟ) were only counted once and assigned to the subplot from which it emerged. In addition to vegetation data, information about litter composition was collected from each subplot. Soil surface matter was classified into four different categories (Table 2). Percentage of covered soil surface by each category was estimated.

Altogether, for each subplot (10 x 10 cm) the following information was gathered:

- Number of different species

- Species cover (percentage of covered ground by above ground biomass of each species)

- Number of abundance units (functional or morphological units) of each species

- Percentage of covered soil surface by each litter category

Table 3: Set of plant traits collected from literature (Source) or derived from the existing data set (footnotes). Numbers in brackets indicate the number of species from the respective source. Different types of variables (Type) include: continuous (1), categorical non-transformed (2), categorical transformed to presence and absence of the trait attributes (3).

Trait	Abbreviation	Type	Trait attributes	Source (number of species)
Maximal height (cm)	Height	1	Continuous	(Fischer, Adler et al. 1994) (36) (Jäger 2007) (1)
Specific leaf area (m² kg⁻¹)	SLA	1	Continuous	Measured value at study site (23) Derived value[1] (14)
Leaf nitrogen content	Leaf N	1	Continuous	(Duvigneaud and Denaeyer-deSmet 1970) (12) (Höhne 1962) (4) (Thompson, Parkinson et al. 1997) (1) Derived value[2] (20)
Leaf lifetime	LLT	3	X1: Evergreen X2: Winter-green X3: Green in summer X4: Partially evergreen	(Ellenberg, Weber et al. 1992) (31) (Jäger and Werner 2002) (6)
Leaf anatomy		2	1: Hygromorphic 2: Hygromorphic to mesomorphic 3: Mesomorphic 4: Mesomorphic to scleromorphic 5: Scleromorphic	(Ellenberg 1974) (35) Derived value[3] (1) Personal observation (1)
Leaf distribution along the stem	LD	3	X1: Rosette/ tufted plant X2: Crown X3: Semi-rosette X4: Regular	LEDA (Kleyer, Bekker et al. 2008) (34) Personal observation (3)
Clonal growth organ	CGO	3	X1: aboveground runners X2: Rhizome X3: belowground storage organs X4: None	LEDA (Kleyer, Bekker et al. 2008) (32) CLO-PLA (Klimesova and Klimes 2007) (3) BIOPOP (Poschlod, Kleyer et al. 2003) (2)
Flowering begin	Flower.begin	1	Continuous	(Fischer, Adler et al. 1994) (37)
Flowering duration	Flower.duration	1	Continuous	(Fischer, Adler et al. 1994) (37)
Dispersal begin		1	Continuous	(Müller-Schneider 1986) (31) Derived value[4] (6)
Dispersal duration		1	Continuous	(Müller-Schneider 1986) (31) Derived value[5] (6)
Diaspore weight		1	Continuous	(Müller-Schneider 1986) (22) SID (Liu, Eastwood et al. 2008) (1) Derived value[6] (14)

[1] Mean value of species with equal leaf lifetime: ANOVA (SLA ~Leaflifetime), p-value: 0.01815 *; R^2= 0.2382; adjusted R^2= 0.2019

[2] Predicted value from Least Square Regression (Leaf N ~maximal height), p-value: 0.0425 *; R^2= 0.2623; adjusted R^2= 0.2097

[3] Mean value of species with equal leaf lifetime: ANOVA (Leafanatomy ~Leaflifetime), p-value: 0.0002183 ***; R^2= 0.3194; adjusted R^2= 0.3005

[4] Predicted value from Least Square Regression (Dispersal begin ~Flowering begin), p-value: 0.000505 ***; R^2=0.3362; adjusted R^2= 0.314

[5] Predicted value from Least Square Regression (Dispersal end ~Flowering end), p-value: 0.0313 *; R^2= 0.1454; adjusted R^2= 0.1169

[6] Predicted value from Least Square Regression (Diaspore weight ~Diaspore length), p-value: 0.00464 ** ; R^2= 0.3367; adjusted R^2= 0.3036

For statistical analysis data was afterwards aggregated to the vegetation plot level by calculating the sums of each species' cover value and abundance units as well as of the litter cover values of all 25 subplots.

Plant nomenclature followed FISCHER, ADLER et al. (2005). In total 37 herbaceous species, including 10 grasses, were considered in the trait analyses. Woody species, mosses, liverworts and ferns were excluded from the analyses.

Environmental data and soil sampling

Variation in spatial plant trait composition and abundance in relation to environmental conditions was analysed with respect to soil pH, soil C:N ratio, humus quality, micro relief, below canopy radiation, and moisture.

Soil pH and soil C:N ratio:

To avoid disturbance of the vegetation plots, soil samples were collected at every corner of the 5 x 5 m grid at both IPs (Figure 5) in May and August 2007. At opposite corners (in cases of paths between plots) samples were only taken from one corner in each case. Again, some sampling points had to be excluded from investigation due to windthrow. At both dates 41 samples were taken from each IP (42 from IP 2 in August). 82 soil samples in May and 83 in August amounted to a total of 165 soil samples, each consisting of a pooled sample of three 5x5x5 cm soil cores. After removal of the litter layer these soil cores were taken exclusively from the A-horizon even if its depth was less than five cm and cores had to be smaller accordingly. For each pooled sample, soil cores were taken at intervals of 50 cm around the sampling corner and displaced 25 cm anticlockwise

in August (Figure 5). In order to remove rough constituents such as litter or rocks, soil samples were sieved using 5mm and 2mm mesh sieves.

Hülber, Dirnböck et al. (2008) showed that the plant species composition of the study area sorts along the acidity and the nitrogen gradient. To represent variations in the nitrogen status due to microbial activity, the ratio of soil carbon to nitrogen (C:N) may be a useful indicator (Janssen 1996; Gundersen, Emmett et al. 1998; Bengtsson, Bengtson et al. 2003). Prior to analyses, homogenized soil samples were laced with hydrochloric acid (37%) for decalcification. C:N ratio was quantified with EA-IRMS (Element analyser isotope ratio mass spectrometer, DeltaPLUS, Thermo Finnigan, Bremen, Germany). Calibration was conducted with an organic standard solution of known concentration. The topsoil pH value was measured in $CaSO_4$-extracts (pH meter, ArgusX, Sentos). Averages of C:N and pH-values of both sampling dates (May and August 2007) were used in statistical analyses.

In order to obtain soil data (pH, C:N ratio) for each vegetation plot, respective values had to be spatially interpolated from the sampling points of the 5m x 5m grids at IP 1 and IP 2. Inverse distance weighting (Philip and Watson 1982; Watson and Philip 1985) was used for this purpose – a method that utilises the dependency of soil parameters from the spatial distance to sampling points. Both IPs were divided into a grid measuring 1m x 1m and values were calculated for each cell by a linearly weighted combination of all sampling points. The resulting interpolated values for pH and C:N ratio were then transferred to the vegetation plots from the cells comprising them.

Humus quality:

pH value and C:N ratio describe the variation of the soil at a scale of meters. Humus however varies at much finer scales and influences the establishment and growth of plants through save sites and decomposition rates. Thus, when analysing the data, we used a simple ratio of the litter cover values of leaves to needles (L:N ratio) in order to account for variation of humus quality (Table 2).

Micro relief:

In terms of humus accumulation it is expedient to assess whether vegetation plots are concave or convex. In order to get information about the shape of the micro-relief at each vegetation plot, a metal bar was applied at the wooden frame for the measurement of distances between the metal bar and the soil surface. Measurements were taken at both ends of the metal bar (20cm outside the frame) and in the centre at the diagonals and the medians of the wooden frame. Values taken from outside the frequency frame were each subtracted from the corresponding centre value, and the resulting eight differences were averaged. Positive values of this index indicate convex, negative values a concave micro-relief.

Below canopy radiation:

Radiation intensity below the canopy was measured with hemispherical photographs that were taken during cloudy con-

ditions using a gimbal at a height of one metre above each plot (Nikon Coolpix 950 camera with a fisheye lens Nikkor 14 mm). At IP 1 all pictures were taken on 2004-08-10 and at IP 2 on 2007-08-08. Total below canopy radiation [W/m²] was calculated from the photographs using the software Gap Light Analyzer (GLA, Version 2.0, Simon Fraser University British Columbia).

Moisture:

A moisture index was derived from the Ellenberg indicator value for soil humidity (Ellenberg, Weber et al. 1992) by calculating the arithmetical mean of the soil humidity indicator values per plot. Prior to this, species cover values at the vegetation plots were transformed to presence/absence data of each species.

While micro-relief and moisture showed normal distribution, L:N ratio, C:N ratio, radiation and pH had to be log-transformed. To achieve improvement in comparability of environmental variables, each variable was centred and scaled by subtracting its mean and subsequently dividing it by its root-mean-square. The root-mean-square for each variable was obtained by computing the square-root of the sum-of-squares of all values divided by the number of values minus one.

Plant traits

For each of the 37 species considered for calculations information on 11 plant functional traits was collected (for references and details on trait definitions see Table 3): maximal height, leaf nitrogen content, leaf lifetime (in the sense of period with foliage), leaf anatomy, leaf distribution along the stem, clonal growth organs, begin of flowering time, duration of flowering time, begin of dispersal time, duration of dispersal time, and diaspore weight (Table 3). In accordance with the state of knowledge documented in literature, such data was not available for every species. Therefore, by taking advantage of the correlations between trait values, missing values were interpolated from the available ones by means of least square regressions (continuous variables) or ANOVA (categorical variables) as described in Table 3.

In addition, existing data on specific leaf area (SLA: the ratio of leaf area to leaf dry mass), measured in July 2005, was used. Methodology of SLA determination followed the standardized procedure as described by Cornelissen, Lavorel et al. (2003). SLA of species that had not been measured in 2005 was derived via ANOVA from the trait data set (Table 3).

Data analyses

We were interested in the prevalence of species along the site gradients independent from their size. Therefore we calculated for each species and vegetation plot the ratio of species cover to the number of abundance units (Table 1). Rock and aboveground root surfaces were taken into account so that species prevalence at the vegetation plots was additionally divided by the sum of leave, needle, and mineral soil cover values (Table 2).

Plant traits included numerical as well as categorical ones (Table 3). Numerical traits were directly incorporated into analyses whereas categorical ones were transformed to presence and absence of the trait attributes afore. Leaf anatomy, though being a categorical trait, was excluded from this kind of transformation
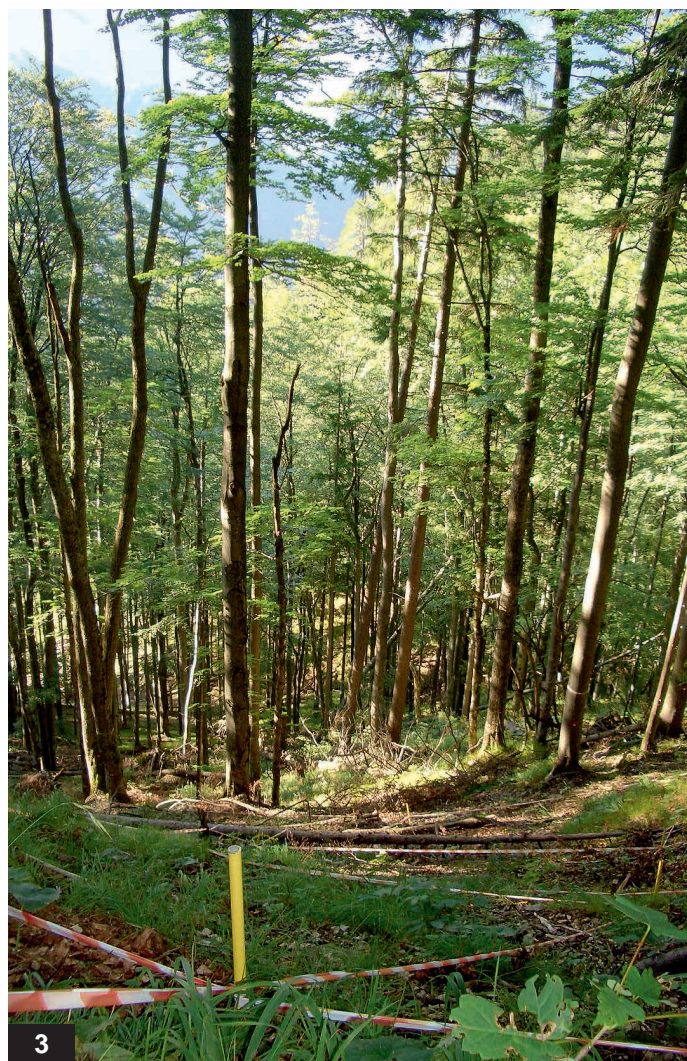
Figure 1: Location of UNECE ICP Integrated Monitoring sites (June 2012). The study area "Zöbelboden" is situated in the Northern Limestone Alps in Austria. Source: UNECE, Finnish Environment Institute: http://www.environment.fi/default.asp?node=6328&lan=en.

Figure 2: Intensive Plot (IP) 1 at the plateau area with Picea abies. 5m grid containing 2 vegetation plots in each square. Source: Umweltbundesamt GmbH, http://www.umweltbundesamt.at.

Figure 3: Intensive Plot (IP) 2 at the slope area with Fagus sylvatica. 5m
grid containing 2 vegetation plots in each square.

Figure 4: Vegetation plot (0.5 x 0.5m) covered by a wooden frame divided into 25 subplots á 10 x 10cm for the collection of species and litter data.
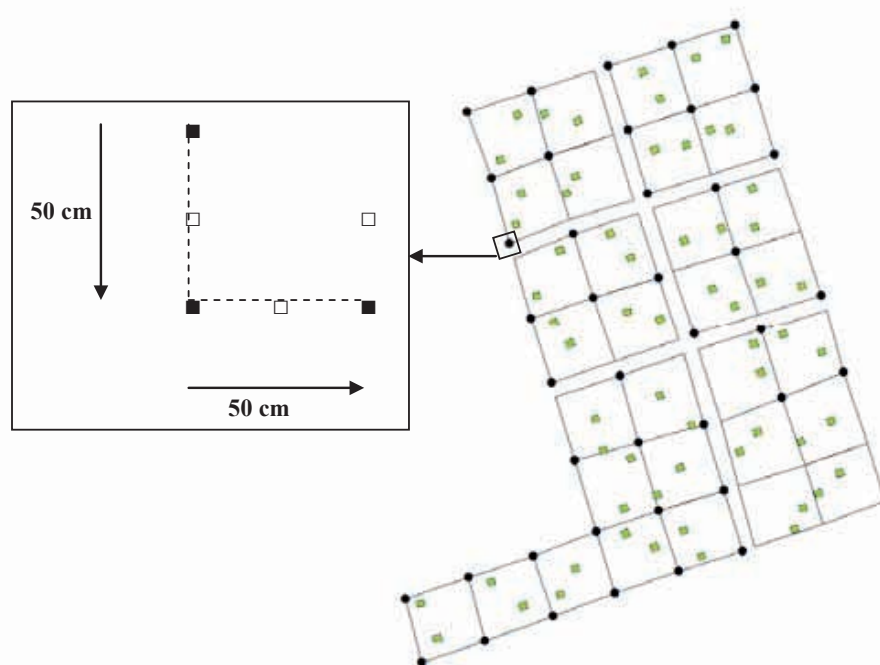
Figure 5: Soil sampling-design at the plateau: At the corners of the 5x5 m grid pooled soil samples (●) consisting of three 5x5x5 cm cores were collected at intervals of 50cm in May 2007 (■) and 25cm displaced in August 2007 (□). Some sampling points had to be excluded owing to windthrow. Squares within the grid represent vegetation plots. Sampling-design at the slope was analogous.

since its attributes were rated on a well-defined ordinal scale. As a consequence of these transformations, the initial trait set was transformed from 12 traits to 9 traits and 12 trait attributes, hereafter likewise referred to and handled as traits.

Relationships between species traits and environmental variables were investigated using RLQ-analyses (DOLÉDEC, CHESSEL et al. 1996). This is a three-table ordination method that examines the joint structure of the matrices R (sites-by-environment matrix) and Q (species-by-traits matrix) linked by the central table L (sites-by-species matrix). The first step in RLQ-analysis consists of a separate analysis of each table. The highest possible correlation between sites and species scores is obtained by the separate correspondence analysis (CA) of the central table L. For the separate analyses of the environmental table R and the trait table Q we chose a multivariate method called Hill-Smith-ordination (HILL and SMITH 1976), which allows quantitative and qualitative variables. Row weights were taken from the site scores of the CA of table L and used as canonical factors. As a result, each environmental variable was positioned at the weighted average of the sites to display habitat structure. Separate analysis of the trait table Q was analogous but with mixed type variables (quantitative and qualitative) and with row weights taken from species scores of the CA of table L to be used as canonical factors. Relationship among traits was shown by positioning each trait (quantitative variables) and trait category (qualitative variables) at the weighted average of the species representing that trait and trait category, respectively.

In the final joint analysis of all three tables, the linking table L is reconstructed with the new set of site scores resulting from Hill-Smith-ordination of table R and species scores resulting from the Hill-Smith-ordination of table Q. Decomposition of the covariance of this cross-matrix provides the RLQ-ordination axes. RLQ-analysis optimizes the covariance between the new sets of site scores modified by environmental attributes and species scores modified by species traits along the first axis and, hence, constitutes a compromise between the three separate ordinations (DOLÉDEC, CHESSEL et al. 1996).

To test the statistical significance of the relationship between R and Q suggested by RLQ analysis a Monte Carlo randomization test was applied. The question is if the total inertia observed in the RLQ analysis is significantly higher ($p<0.001$) than the values obtained by the permutations, thus if there is significant link between tables R and Q through table L.

We used the software R 2.4.0. (http://www.r-project.de) for data analyses with the library "ADE-4" for the RLQ-analysis.

Results

Separate analysis of habitat structure

In the separate analysis of environmental variables, total variance was primarily represented by ordination axis one compared to axis two, which only accounted for around half as much of the variation (Table 4, Figure 6). Variables most correlated with axis one were soil pH, C:N ratio, moisture, and the litter ratio of leaves to needles. Relief was most strongly correlated with axis two whereas all other variables showed low correlation with axis two (Table 4). The first axis distinguished acidic, moist sites with less available nitrogen and predominately needles in the litter layer (left side) from alkaline, dry sites with higher amounts of available nitrogen and leaf litter (right side). The second axis represented plots from convex (above) to concave (below) relief forms. Below canopy radiation was higher at the plots with concave relief, although this trend is weak (Figure 6).
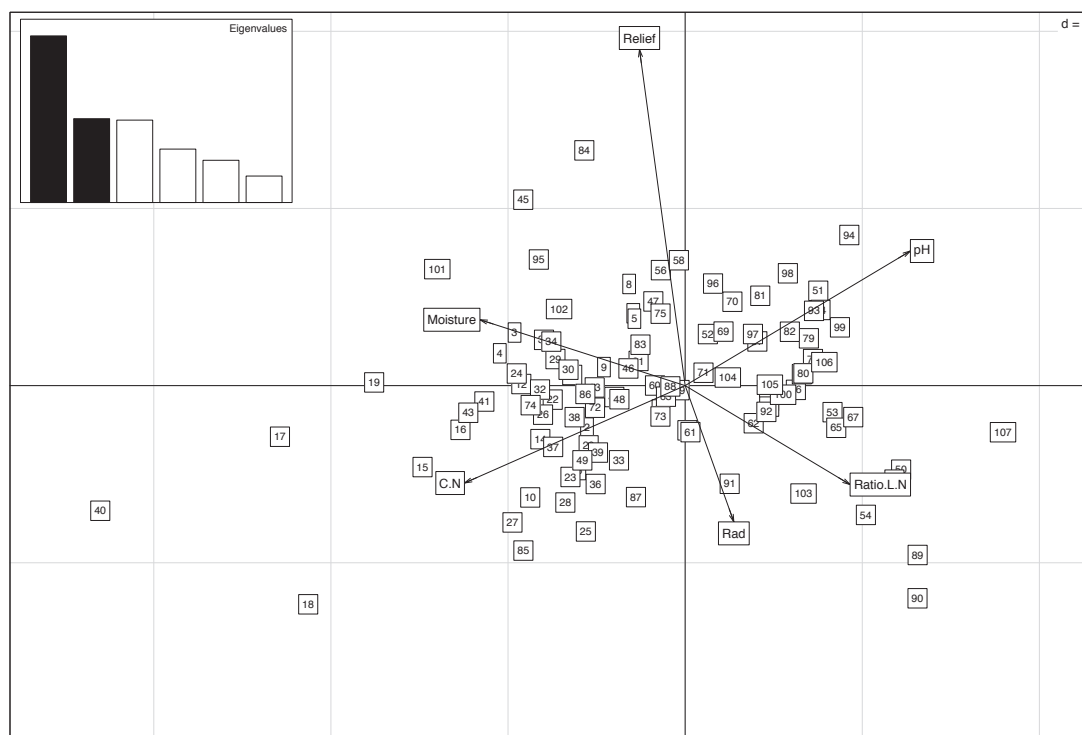
Figure 6: Habitat structure: Separate ordination of sites and environmental variables (table R: sites-by-environment) by Hill-Smith-ordination. Environmental variables along the first two ordination axes displaying environmental gradients, distribution of the 107 surveyed sites (numbered squares). Each environmental variable is positioned at the weighted average of the sites (row weights taken from the site scores of the CA of table L were used as canonical factors). Note that the first axis nearly accounts for twice the amount of total variance as indicated by the upper-left insert (eigenvalues of the ordination).

Separate analysis of the relationship among species traits

In the Hill-Smith-ordination of the traits table, the first axis accounted for nearly twice the amount of total variance compared to axis two (Table 5). Correlations along the first two ordination axes were given by squared correlation ratios for quantitative traits and correlation ratios for qualitative traits (Table 5). Nine out of 12 traits showed stronger correlation with the first axis, at which the highest correlations were given by leaf lifetime, diaspore weight, flowertime begin, leaf nitrogen, and maximal height. Highest correlations along the second axis were rendered by dispersal duration, leaf anatomy, and clonal growth organs (Table 5). Trait associations distinguished along the first axis were early flowering species with short stature, long-lived leaves, weighty diaspores, and low leaf nitrogen content, on the one hand, and tall-growing, late-flowering species with light weighted diaspores and short-lived leaves with high SLA values as well as high leaf nitrogen content, on the other hand. The second axis opposed hygromorphic plants with long dispersal duration and below ground clonal growth organs to rather scleromorphic plants with shorter dispersal periods and aboveground vegetative spread (Figure 7).

Joint analysis of environmental variables and species traits: RLQ analysis

In RLQ analysis, most information was given by the first axis as it accounted for a ten times higher amount of total variance of

the RLQ model than the second axis (Table 6a).

The covariance between new site scores modified by environmental attributes and new species scores modified by the species traits was optimized along the first RLQ axis and was considerably higher than along the second axis (Table 6a).

Correlation between modified site and species scores was also higher along the first RLQ axis than along the second RLQ axis. To estimate the goodness of fit of the RLQ model, called "Correlation L" (DOLÉDEC, CHESSEL et al. 1996), the maximal potential correlation between site and species scores given by the initial CA of table L was compared to the correlation achieved by the RLQ model along the first axis. As a result, RLQ analysis took into account a large proportion of the co-structure of the initial sites-by-species table (Table 6c).

Compared to separate ordinations of tables R and Q, the first RLQ axis accounted for the most part of the variance of environmental variables obtained by separate analysis of table R, just as of the variance of traits obtained by separate analysis of table Q (Table 6b). With addition of the second RLQ axis, the proportion of projected variance by RLQ analysis declined (table R) or only showed an unremarkable increase (table Q) in comparison to axis one only. Thus, the proportion of information extracted on the second RLQ axis is negligible and only the first axis will be considered in detail.

The Monte Carlo test reinforced the significance of the link between table R and table Q suggested by the RLQ model (p=0.001, based on 999 replicates), thus the results of RLQ anal-

ysis validly represented the relationship between environmental conditions and biological traits.

Relationship between environmental conditions and species traits

Habitat structure displayed by RLQ analysis (Table 7, Figure 8) resembled that described by separate analysis of table R (Table 4, Figure 6). A pH-nitrogen gradient along RLQ axis one exhibited a transition from acidic conditions with less available nitrogen on the negative end to alkaline, high nitrogen environments towards the positive end. RLQ axis one furthermore separated environments predominated by conifers (mainly needle litter), low below canopy radiation and high moisture from those characterised by deciduous trees (mainly leaf litter), high radiation and less moist conditions. The former habitats were associated with acidic, nitrogen poor conditions on the left end of the pH-nitrogen gradient, the latter with rather alkaline sites with higher amounts of available nitrogen on opposite end. Micro-relief showed comparatively low scores along both RLQ axes (Table 7), although it was highly correlated with axis two in separate analysis (Table 4). Concave micro-relief characteristics were positioned towards the positive end of the pH-nitrogen gradient, which corresponds to alkaline, high nitrogen environments (Figure 8).

RLQ ordination clearly demonstrated different trait combinations in relation to environmental characteristics (Table 7, Figure 8). On the left part of RLQ axis one, coinciding with low nitrogen availability and moist, acidic soils, herbs of taller stature and lush leaf development (hygromorphic, summer-green, high SLA, high leaf nitrogen content) were accumulated. These plant traits were as well associated with light weighted seeds, clonal growth (if any) by aboveground runners, and a regular leaf distribution along the stem or leaves concentrated as a crown at the top of a taller shoot or vegetative stem. Late begin of flowering and dispersal and, at the same time, short flowering and dispersal duration were further plant characteristics at those habitats. Species located on the very negative end of RLQ-axis one were, for example, Purple Lettuce (*Prenanthes purpurea* L.), Raspberry (*Rubus idaeus* L.), and Reedgrass (*Calamagrostis varia* (SCHRAD.) HOST) (Table 8).

By contrast, traits aggregated on the right end of RLQ axis one (nitrogen-rich, alkaline, and less moist conditions) included short stature, early and long flowering as well as dispersal periods, and below-ground storage organs. There were evergreens with thick and robust leaves (scleromorphic leaf anatomy, low SLA) concentrated in tufts or rosettes. Species located on the very right end of RLQ axis one were, for example, Christmas Rose (*Helleborus niger* L.), *Sesleria albicans* KIT. ex SCHULT. , and False Aster (*Bellidiastrum michelii* CASS.) (Table 8).

Table 4: Separate ordination of environmental variables: Eigenvalues and percentages of the total variance accounted for by the first two axes of the ordination of table R (sites-by-environment), squared correlation coefficients for each environmental variable along the same axes. Environmental variables are given in descending order of their correlation along ordination-axis one. Soil pH value and C/N ratio stem from the top 5 cm of the mineral soil; moisture index: increasing values indicate increasing moisture; Humus ratio L/N: ratio leaves to needles cover value per vegetation plot (Table 2); below canopy radiation: total below canopy radiation [W/m²]; relief: values > 0 indicate convex relief conditions at the vegetation plot and values < 0 indicate concave ones.

	Axis 1	Axis 2
Eigenvalue (% total variance)	2.20 (36.62%)	1.11 (18.43%)
Soil pH-value	0.644	0.116
Soil C/N ratio	0.618	0.061
Moisture index	0.534	0.028
Humus ratio L/N	0.345	0.062
Below canopy radiation	0.030	0.118
Relief	0.026	0.721

Table 5: Separate ordination of species traits: Eigenvalues and percentages of the total variance accounted for by the first two axes of the Hill-Smith-ordination of table Q (species-by-trait), squared correlation coefficients for quantitative traits and correlation ratios for qualitative traits along the same axes. Traits are given in descending order of correlation along ordination-axis one. For details of trait attributes see Table 3.

	Axis 1	Axis 2
Eigenvalue (% total variance)	4.56 (25.31%)	2.29 (12.73%)
Leaf lifetime	0.624	0.201
Diaspore weight	0.610	0.050
Flowering begin	0.533	0.035
Leaf nitrogen content	0.456	0.040
Maximal Height	0.449	0.130
Dispersal begin	0.408	0.030
Specific Leaf Area	0.398	0.068
Flowering duration	0.374	0.249
Leaf distribution along the stem	0.341	0.266
Leaf anatomy	0.305	0.419
Dispersal duration	0.056	0.546
Clonal Growth Organs	0.001	0.256

Discussion

Trait linkages and trade-offs

In the present study RLQ ordination displayed clearly segregated patterns of species traits, namely a trade-off between traits associated with a high capacity of resource acquisition, on the one hand, and traits conducive to resource conservation, on the other hand. Trait sets indicative for high investment in photosynthesis and rapid growth, such as high SLA, high leaf N content, and short leaf lifetime were located on the left part of the ordination axis. By contrast, trait combinations at the opposite end of the ordination axis are associated with the retention of captured resources and the investment into defence and included below-ground storage organs, long-lived leaves, and a robust
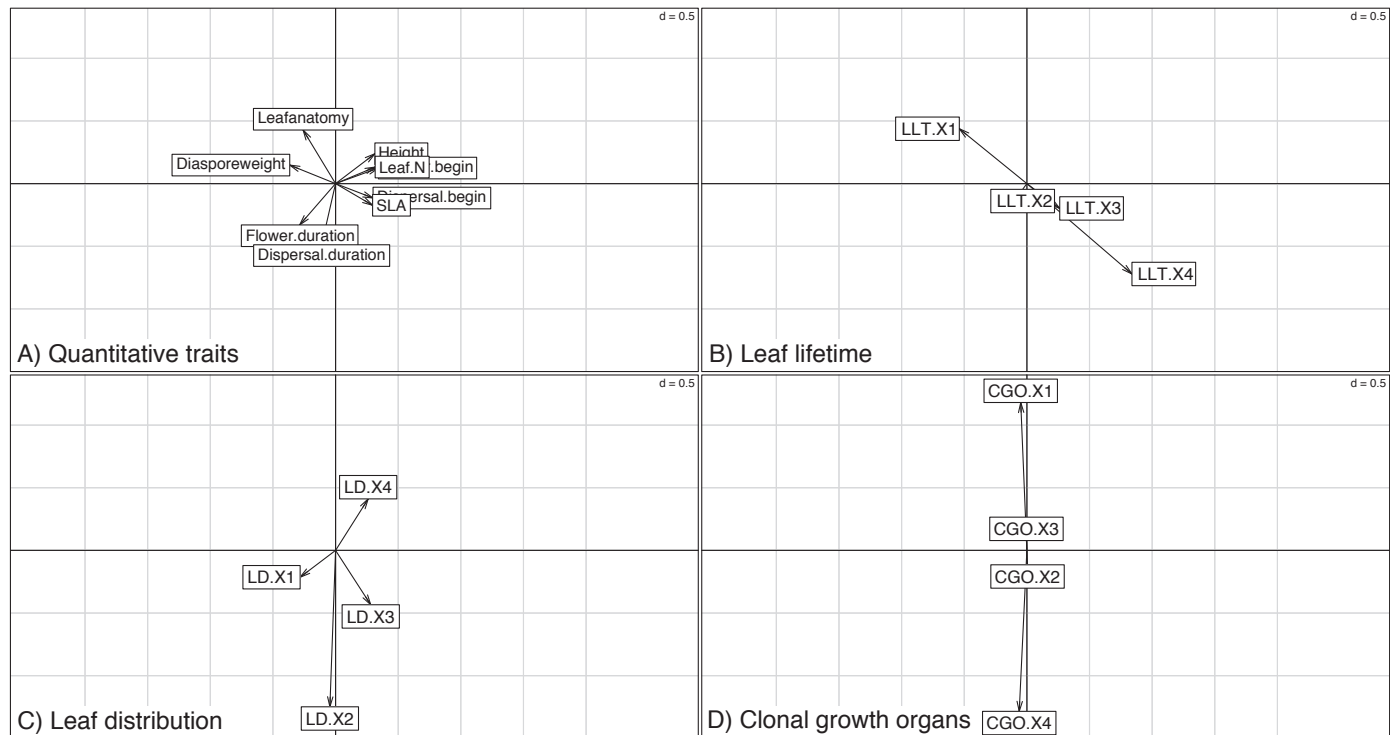
Figure 7: Relationship among biological traits: Separate ordination of species and traits (table Q: species-by-traits) by Hill-Smith-ordination. Display of quantitative traits (A) and trait categories of factorial traits (B-D) along the first two ordination axes indicating relationships among traits and trait categories, respectively. The points are in the middle of the labels. Partly overlapped labels: "Flower.begin", "Dispersal.begin" (see scores Table 5). Each trait and trait category is positioned at the weighted average of the species representing that trait or trait category (row weights taken from the species scores of the CA of table L were used as canonical factors). Note that the first axis nearly accounts for twice the amount of total variance (Table 5). d: scale of the grid. For details and abbreviations of the traits see Table 3.
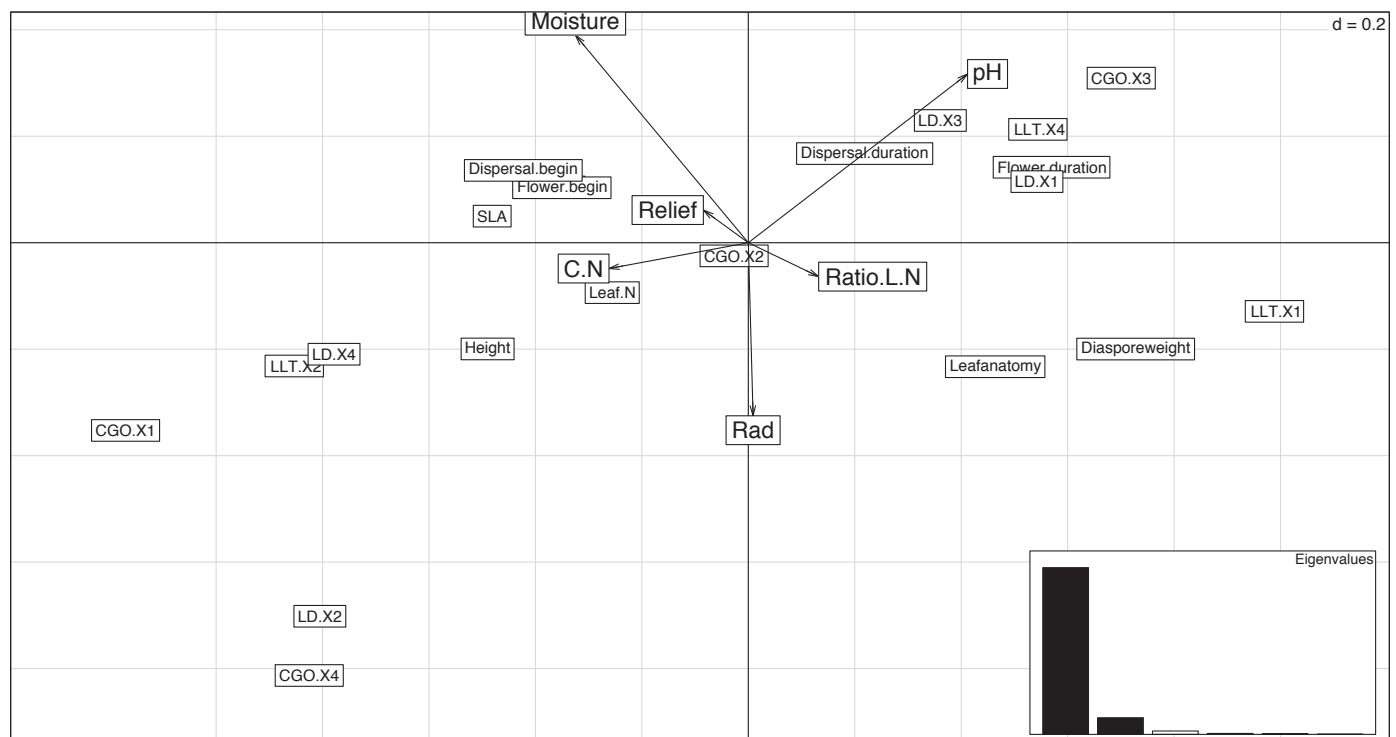

Figure 8: RLQ-analysis: Relationship between plant traits and environmental factors. The points are in the middle of the labels. Partly overlapped labels: "LLT.X2", "Flower.duration", fully overlapped label: "LLT.X3" (see scores Table 7). For details and abbreviations of the traits see Table 3. d: scale of the grid. Note that the first axis accounts for the most part of total variance as indicated by the lower-right insert (eigenvalues).

Table 6: Summary of RLQ analysis: **a)** RLQ model: eigenvalues of the first two axis resulting from RLQ analysis and percentages of the total variance accounted for by each axis; covariance and correlation between the modified set of site scores and species scores projected onto the first two RLQ axes **b)** Comparison of the projected variances of the two sets of site and species scores resulting from the separate ordinations of table R (sites-by-environment) and of table Q (species-by-trait), respectively, and the RLQ analysis: eigenvalues of the first axis and the sum of the first two axes of each corresponding ordination; percentages of the total variance accounted for by RLQ axis 1 and by the sum of RLQ axis 1 plus axis 2. **c)** Comparison of the correlation between site and species scores along the first axis obtained by the separate CA of table L (sites-by-species) and the cross-correlation obtained by RLQ analysis; percentage of the maximal correlation achieved by RLQ analysis (goodness of the estimated solution).

a) RLQ analysis	RLQ-Axis 1	RLQ-Axis 2
Eigenvalue (% total variance)	2.97 (88.40%)	0.30 (8.83%)
Covariance	1.72	0.54
Correlation	0.60	0.40
b) Comparison of projected variance	**Axis 1**	**Axis 1+ 2**
table R (separate ordination)	2.20	3.30
table R (RLQ analysis)	2.08	3.00
% RLQ	94.80	90.85
table Q (separate ordination)	4.56	6.85
table Q (RLQ analysis)	3.94	5.98
% RLQ	86.53	87.32
c) Comparison of correlation	**Axis 1**	
table L (separate CA)	0.90	
RLQ analysis	0.60	
% RLQ	66.99	

leaf anatomy for the protection from unfavourable environmental conditions (Figure 8). These basic trait associations are in line with findings of previous studies and have been documented for various biomes and a broad range of ecological spectra (GRIME 1977; CHAPIN 1980; REICH, WALTERS et al. 1992; DÍAZ and CABIDO 1997; GRIME, THOMPSON et al. 1997; DÍAZ, HODGSON et al. 2004). Analogous functional shifts were also shown between communities differing in successional status (KAZAKOU, GARNIER et al. 2007; NAVAS, ROUMET et al. 2009).

Environment – trait associations

All in all, a high percentage of variance of environmental as well as trait variables was projected along the first RLQ axis and, furthermore, an adequate goodness of fit was rendered by the RLQ model. From this follows that the RLQ model was able to properly excerpt the common structure of tables R and Q through table L, that is the relationship between environmental variables and species traits in the area under investigation (Table 6, Figure 8).

However, the nitrogen gradient along the first RLQ axis ran counter to expectations, inasmuch as traits positioned at low soil nutrient availability (high C:N ratio on the left-hand side of RLQ-axis one) would actually be associated with nutrient rich habitats and vice versa. High SLA values and leaf N content are usually found at sites rich in nutrients (WESTOBY 1998; GRIME

2001; KAHMEN and POSCHLOD 2004). Our result may be due to the comparatively narrow range of the C:N ratio values (13-18, once 20) encountered at the investigated vegetation plots causing a weakening of correlations (LAVOREL and GARNIER 2002). Alternatively, in view of the small-scale vegetation analysis the soil sampling scale (5 m grid) might be inappropriate to account for the characteristically small-scale variability of soil nitrogen content known for temperate deciduous forest soils (FARLEY and FITTER 1999) or of humus conditions in mixed spruce forests (KARRER and ENGLISCH 1998). It has been documented that nitrate and ammonium concentrations vary considerably in dimensions of only 20cm (FARLEY and FITTER 1999). In general, consideration of scale in relation to the spectrum of the investigated environment is of vital importance in the interpretation of trait linkages and trade-offs (LAVOREL and GARNIER 2002).

It has been shown for the study area that nitrogen availability in the soils have some potential to control tree establishment (DIWOLD et al. 2010, PRÖLL et al. 2011). However, nitrogen limitation is unlikely to be a strong environmental filter for vascular plants at the majority of sites of the study area. Long-term observations from 1992 to 2005 showed that nitrogen availability is generally sufficient and favourable for plant growth in the area and only sites which are particularly dry and base rich or moist and acidic experienced effects due to excess nitrogen deposition (HÜLBER, DIRNBÖCK et al. 2008). Latter sites are missing in our data set so that nitrogen does not play a major role in trait specification. If nitrogen was not the predominating factor for

Table 7: Normed scores of environmental variables and plant traits on the first two axes resulting from RLQ analysis (Figure 8). Variables and traits are given in ascending order according to their scores along RLQ-axis one. For details and abbreviations of the traits see Table 3.

	RLQ axis 1	RLQ axis 2
Environmental variables		
Moisture index	-0.535	0.643
Soil C/N ratio	-0.431	-0.08
Relief	-0.139	0.101
Below canopy radiation	0.015	-0.536
Humus ratio L/N	0.218	-0.105
Soil pH-value	0.679	0.522
Species traits		
CGO.X1: aboveground runners	-0.679	-0.647
LLT.X2: Winter-green	-0.495	-0.425
CGO.X4: None	-0.478	-1.492
LD.X2: Crown	-0.467	-1.288
LD.X4: Regular	-0.451	-0.385
Maximal height	-0.284	-0.366
SLA	-0.279	0.092
Dispersal time begin	-0.245	0.249
LLT.X3: Green in summer	-0.210	0.192
Flowering time begin	-0.203	0.190
Leaf nitrogen content	-0.148	-0.172
CGO.X2: Rhizome	-0.015	-0.045
Dispersal duration	0.127	0.307
LD.X3: Semi-rosette	0.209	0.421
Leafanatomy	0.269	-0.428
LD.X1: Rosette/ tufted plant	0.315	0.211
LLT.X4: Partially evergreen	0.316	0.391
Flowering duration	0.330	0.260
CGO.X3: belowground storage organs	0.406	0.567
Diaspore weight	0.422	-0.367
LLT.X1: Evergreen	0.573	-0.237

functional differentiation, what sort of constraints would underlie species trait arrangement, then?

Considering site scores along the first RLQ axis a clear separation of vegetation plots situated at the plateau area (IP 1) from those at the slope area (IP 2) becomes evident (Figure 9). Plateau plots were exclusively located on the left side of the RLQ ordination plane, coinciding with acidic and moist environmental conditions. On the other hand, nearly all slope plots were positioned at the positive part of the first RLQ axis towards rather alkaline and less moist environments (Figure 9). The separation of these two subareas along the first RLQ axis corresponds to the trade-off between investments into resource acquisition and, on the other hand, allocation to storage and defence as described above. Obviously, there occurs a functional shift from plant communities primarily specialising in resource acquisition (tall plants with short-lived leaves characterised by high SLA, as well as high leaf nitrogen content) at the plateau to communities rather adapted to conservation and defence (drought-resistant, long-lived leaves with low SLA, storage organs, and short-stature) at the slope.

Fast growing plants at the acidic plateau displayed higher foliar nutrient concentrations (high leaf nitrogen content) – an indication of the tendency of those plants to activate mineral resources to boost metabolism. Positive correlation between foliar concentration of nitrogen and SLA has been documented repeatedly for a wide range of different habitats (GRIME, THOMPSON et al. 1997; REICH, ELLSWORTH et al. 1999; HOFFMANN, FRANCO et al. 2005), just as both high SLA and high leaf nitrogen values in conjunction with low soil pH (HOFFMANN, FRANCO et al. 2005; KÜHNER and KLEYER 2008). However, the reverse relationship between low pH and leaf nitrogen content would be expected as acidic conditions are known to reduce nitrification (VITOUSEK and MATSON 1985; PERSSON and WIREN 1995). HOFFMANN, FRANCO et al. (2005) put their results into the context of findings that showed an increase of leaf nitrogen content with higher soil NH_4^+ concentrations in proportion to NO_3^- (GARTEN 1993) owing to low soil pH (BIGELOW and CANHAM 2002). Nevertheless, at our study site low pH values are unlikely to explain high leaf nitrogen content, rather this may be due to the known higher availability of nitrogen for plant growth at the plateau (PRÖLL et al. 2011), which in turn may be a consequence of higher moisture at those habitats (TIETEMA, WARMERDAM et al. 1992) (Figure 8).

Water use efficiency has been related to low SLA values since high relative leaf water content is supported by a reduced leaf area (WRIGHT, NAGESWARA RAO et al. 1994; NAUTIYAL, NAGESWARA RAO et al. 2002; ANYIA and HERZOG 2003; HOFFMANN, FRANCO et al. 2005). Our results are in accordance with these findings in that low SLA plants increased contrary to the moisture gradient (Figure 8). In our analysis, the slope area turned out to be a rather drought habitat compared to plots at the plateau and low SLA was found, accordingly, most notably at the slope. In addition, an evident transition between hygromorphic to scleromorphic leaf anatomy was observed from the plateau to the slope, as well as an increase of evergreens, heavy seeds, and dominance of tufted and rosette habitus. These characteristics have been referred to as drought adaptive (REYNOLDS, SKOVMAND et al. 2000; GRIME 2001).

SLA reduction in response to decreasing moisture may as well be due to differences in total below canopy radiation since humidity is always correlated with light intensity. We found SLA negatively correlated with total below canopy radiation, although this relationship was less obvious for it was displayed on the second RLQ-axis, which only accounted for 8,83 % of total variance. However, in forest succession from semi-open woodland to closed deciduous forest canopy an increase in species possessing high SLA has been observed (DAHLGREN, ERIKSSON et al. 2006), thus indicating that low light environments favour species adapted to lower evapotranspiration rates via high investment into photosynthetic tissue. In this context, high SLA has been associated with slow-growing shade plants (WILSON, THOMPSON et al. 1999; GRIME 2001; DAHLGREN, ERIKSSON et al. 2006). Moreover, in shaded habitats such as forests competition for light rather than mineral nutrients seems to be the decisive factor with regard to SLA characteristic (WILSON, THOMPSON et al. 1999; KAHMEN and POSCHLOD 2004; DAHLGREN, ERIKSSON et al. 2006). Generally, soil moisture and air humidity have been proven to be the crucial factors in determining herb cover of temperate beech forests on calcareous soils (LEUSCHNER and LENDZION 2009).

Plant strategies

In C-S-R theory, individual selective factors such as those described above can be combined into two main ecological factors, resource stress and disturbance, in order to classify plants into functional groups according to their evolutionary strategy (GRIME 1977). At the plateau area, disturbance seems to more pronounced as a result of former forestry. Furthermore, recent tree harvesting in consequence of bark beetle infestation produced gaps in the otherwise dense tree canopy. According to Grime's C-S-R model, functional shifts along increasing disturbance intensities tend to result in an increase of ruderal plant characteristics within the plant communities (GRIME 1977; HODGSON 1991).

In the present study, the first ordination axis delineated different plant strategies between the plateau and the slope. These strategies are related to the species' traits and express the linkages and trade-offs between traits in response to varying intensities of resource stress and disturbance. Most species at the study area exhibited secondary strategies, that is trait attributes at intermediate levels of C (competitive), S (stress-tolerant), or R (ruderal) characteristics (GRIME 2001). The trait associations on the left-hand side of the RLQ ordination plane were in accordance with the characteristics of CSR strategists for the most part, while stress-tolerance (SC and S strategists) took on greater significance towards the other end of the RLQ plane.

CSR strategists are characteristic of habitats with intermediate seasonal or spatial variations of stress and disturbance (GRIME 2001). Representatives of the CSR strategy, such as *Senecio ovatus* (G. GAERTN. & al.) WILLD. and Yellow pimpernel (*Lysimachia nemorum* L.), were concentrated at the plateau area, which consisted of acidic and moist habitats. The morphological trait spectrum of these plants comprised a tall stature, leaves either distributed regularly along the stem or concentrated as a crown at the top of taller shoots or vegetative stems, and above-ground runners as clonal growth organs (Table 8, Figure 8). Such a creeping or stoloniferous morphology is a characteristic feature of CSR strategists that exploit gaps in herbaceous canopies by their ability to root at advantageous soil patches but photosynthesise at displaced gaps (GRIME 2001). A real master in managing with the dense forest understorey is Yellow Archangel (*Galeobdolon montanum* (PERS.) PERS. ex RCHB.) by its vegetative "arched shoots" that firstly sprout erectly up to 0.5 to one meter but subsequently sink to the forest floor for rooting. The species, thereby, reaches distant gaps in the herbaceous layer and is able to bridge ground-covering as well as moderately tall-growing competitors (KARRER 1997).

An equivalent explanation has been proposed for strategies of creeping plants dealing with high accumulations of tree litter (GRIME 2001). Woodruff (*Galium odoratum* (L.) SCOP.), for instance, develops decumbent shoots that take roots at the nodes, when pressed down onto the leaf litter by the covering snow. In this manner, expansion to micro-environments of extremely high leaf litter accumulation is possible, while germination favourably happens at low litter micro-habitats. This strategy is optimal to cope with high leaf litter production in temperate beech forests as well as unequally distributed litter accumulations pertaining to wind-driven processes, which is a frequent phenomenon at our study site (KARRER 1997).

Additional features of the species concentrated towards the negative end of RLQ axis one were high SLA values as well

Table 8: Normed species scores along the first two RLQ axes: Species in ascending order according to their scores along RLQ-axis one.

Species	RLQ-axis 1	RLQ-axis 2
Prenanthes purpurea	-1.213	0.465
Rubus idaeus	-1.128	-0.971
Calamagrostis varia	-1.062	-0.282
Senecio ovatus	-1.043	0.718
Lysimachia nemorum	-0.997	0.386
Brachypodium sylvaticum	-0.907	0.968
Polygonatum verticillatum	-0.871	-0.216
Daphne mezereum	-0.830	-1.676
Oxalis acetosella	-0.800	0.751
Carex pendula	-0.712	-0.149
Cardamine trifolia	-0.630	-0.889
Mercurialis perennis	-0.606	-0.706
Hordelymus europaeus	-0.597	0.095
Galium odoratum	-0.584	-0.198
Adenostyles alpina	-0.524	0.606
Galeobdolon montanum	-0.504	-1.705
Galium rotundifolium	-0.464	0.129
Carex sylvatica	-0.347	0.006
Phyteuma spicatum	-0.265	0.697
Fragaria vesca	-0.170	0.146
Luzula pilosa	-0.131	0.200
Sanicula europaea	-0.107	0.329
Actaea spicata	0.021	1.445
Knautia maxima	0.120	1.730
Viola reichenbachiana	0.128	0.788
Primula elatior	0.133	1.491
Daphne laureola	0.221	-2.629
Valeriana tripteris	0.426	1.418
Carex flacca	0.435	0.787
Carex alba	0.435	0.453
Asarum europaeum	0.529	-0.375
Carex digitata	0.568	-0.060
Euphorbia amygdaloides	0.579	0.083
Cyclamen purpurascens	0.699	0.743
Bellidiastrum michelii	0.812	1.366
Sesleria albicans	0.853	-0.334
Helleborus niger	1.942	-1.175

as high leaf nitrogen content, short-lived and hygromorphic to mesomorphic leaves, late begin of flowering and dispersal, and light weighted diaspores – a trait combination indicative of ruderal strategy (Figure 8) (GRIME 2001). At the plateau recent single tree harvesting produced canopy gaps with elevated light supply, which could have been beneficial for species with ruderal adaptation. Good colonizing capacities of plants with equivalent traits were shown for European and North-eastern American forests, where small seeded, perennial herbs and small, summer flowering, vegetatively spreading graminoids demonstrated the best colonizers (VERHEYEN, HONNAY et al. 2003). Moreover, SLA has been identified as an indicator for relative growth rate (REICH, WALTERS et al. 1992; REICH, ELLSWORTH et al. 1999; WRIGHT, REICH et al. 2004). In our study, fast-growing plants could optimally exploit these emerging patches below canopy gaps just as the short growing season at late-melting habitats
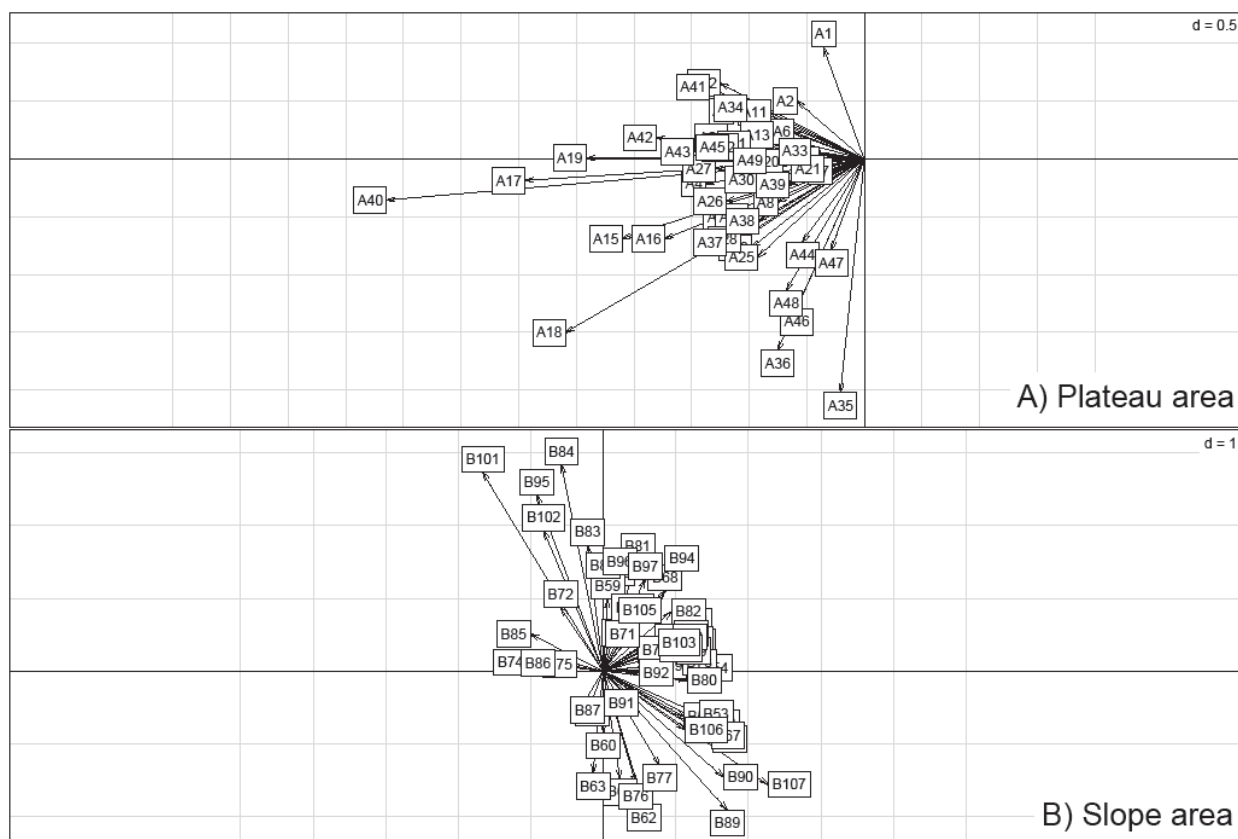
Figure 9: Separation of vegetation plots at the plateau area (A) on the left part and those at the slope area (B) mainly on the right part of the RLQ-ordination-plane. Horizontal axis: RLQ-axis one, vertical axis: RLQ-axis two. Labels (squares) of vegetation plots at the plateau (A1-A49) and the slope area (B50-B107). d: scale of the grid.

in alpine grassland is managed by fast-growing plants of high SLA and reduced seed mass (CHOLER 2005). Altogether, plant response to environmental conditions at the plateau comprised besides intermediate CSR strategists also a tendency towards ruderal features in SR species (stress-tolerant ruderals) such as *Adenostyles alpina* (L.) BLUFF & FINGERH.

Towards the other end of RLQ axis one, disturbance apparently became less important whereas stress-tolerant characteristics tended to come to the fore. In contrast to the anthropogenic influenced plateau with mainly CSR strategists, the understorey vegetation at the slope, with its natural vegetation of a mixed montane forest, was characterised by a higher amount of stress-tolerant features (Table 7, Figure 8). Specific storage organs, weighty diaspores, evergreenness, scleromorphic leaves, as well as low SLA and short stature have been associated with the stress tolerant strategy, and resource conservation rather than rapid growth (GRIME, THOMPSON et al. 1997; WESTOBY 1998; GRIME 2001; WRIGHT, REICH et al. 2004). In the RLQ ordination plane SC (stress-tolerant competitors) such as evergreen Spurge-laurel (*Daphne laureola* L.), SR (stress-tolerant ruderals) including geophytes such as *Cyclamen purpurascens* MILL., and S

strategists (primary stress-tolerant plants) represented by monocots like Blue Sedge *(Carex flacca* 'SCHREB.) were aggregated at the positive end of the first axis (Table 8, Figure 8). As mentioned earlier, the water use efficiency of plants, which differed between the moist plots at the plateau and the rather drought plots at the slope, was linked to stress-tolerant plant attributes such as low SLA, scleromorphic leaf anatomy, and evergreenness. A functional shift from plant trait combinations including high SLA and short leaf lifespan to those including low SLA and evergreenness along a gradient of increasing water stress has already been demonstrated on a broader scale of climatic conditions (DÍAZ and CABIDO 1997; DÍAZ, CABIDO et al. 1998). It is, however, important to note the occurrence of S strategists also at the plateau area, although stress tolerance of those plants is not based on limited water supply, but rather originates from the ability of species such as Common Wood-sorrel (*Oxalis acetosella* L.), Hairy Wood rush (*Luzula pilosa* (L.) WILLD.), or Trefoil Cress (*Cardamine trifolia* L.) to cope with shade (GRIME 2001). Indifferent position of the rhizome category in the RLQ ordination implied that clonal growth through rhizomes seems to be a common feature of the herbaceous understorey in both habitats of the examined forest (Figure 8).

Perspectives

RLQ analysis proved to be a convenient and powerful tool for the simultaneous analysis of plant traits and ecological factors. It clearly separated different plant strategies (GRIME 1977) and was able to display the fundamental trade-off between investment into photosynthesis and resource acquisition versus allocation to storage and defence (GRIME 1977; CHAPIN 1980; REICH, WALTERS et al. 1992; DÍAZ and CABIDO 1997; GRIME, THOMPSON et al. 1997; DÍAZ, HODGSON et al. 2004; KAZAKOU, GARNIER et al. 2007; NAVAS, ROUMET et al. 2009).

Nevertheless, the question which traits are the most responsive to the given environmental circumstances and which trait set is most qualified for application in plant functional trait analyses remains. Recent efforts to account for this question include a new recursive optimization algorithm to select relevant traits and to find optimal plant functional types by numerical analysis (PILLAR and SOSINSKI 2003) and a new three step method (logistic regression, iterative clustering, selection of best fitted trait combination) to search for the smallest number of functional traits sufficient to predict plant response to varying environmental conditions (KÜHNER and KLEYER 2008). A very promising approach in combination with RLQ analysis was suggested by BERNHARDT-RÖMERMANN, RÖMERMANN et al. (2008), who formulated the method of iterative RLQ-analysis, which selects the most relevant trait combination with the most parsimonious number of traits prior to trait-environment analysis itself.

Acknowledgements

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